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MODIS enhanced vegetation index predicts tree species richness across forested ecoregions in the contiguous U.S.A.

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Abstract

With the expectation of major shifts in climate, ecologists have focused attention on developing predictive relationships between current climatic conditions and species diversity. Climatic relationships appear best defined at regional rather than local levels. In reference to tree diversity, process-based models that express gross primary production (GPP) as an integrated function of climate seem most appropriate. Since 2000, NASA's MODIS satellite has provided composite data at 16-day intervals to produce estimates of GPP that compare well with direct measurements. The MODIS enhanced vegetation index (EVI), which is independent of climatic drivers, also appears a good surrogate to estimate seasonal patterns in GPP. In this paper we identified 65 out of 84 delineated ecoregions distributed across the contiguous U.S.A., within which sufficient (≥ 200) Federal Inventory and Analysis survey plots were available to predict the total number of tree species, which varied from 17 to 164. Four different formulations of EVI were compared: The annual maximum, the annual integrated, the growing season defined mid-point and growing season averaged values. The growing season mid-point EVI defined the beginning and end of the active growing season. In all formulations of EVI, a polynomial function accounted for about 60% of the observed variation in tree diversity, with additional precision increasing to 80% when highly fragmented ecoregions with <50% forest cover were excluded. Maps comparing predicted with measured tree richness values show similar patterns except in the Pacific Northwest region where a major extinction of tree genera is known to have occurred during the late Pliocene. The extent that these relationships remain stable under a changing climate can be evaluated by determining if the MODIS climate-driven estimate of GPP continues to match well with EVI patterns and systematic resurveys of forest vegetation indicate that tree species are able to adjust rapidly to climatic variation.
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1. Introduction

Over the last few decades, there has been an expanded effort to predict biological diversity as a function of climate at both the regional (Currie & Paquin, 1987; Hawkins et al., 2003; O'Brian, 1998; Venevsky & Veneskaia, 2003) and global scale (Gaston, 2000; Kleidon & Mooney, 2000; Latham & Ricklefs, 1993). This expanded interest is justified on the basis of accelerated

extinction and the expectation that a major reconfiguration of vegetation patterns is predicted during this century (Iverson & Prasad, 2001). The paleobotanical record provides evidence that a changing climate obliterates major associations and causes new ones to be formed (Axelrod et al., 1991). For this reason most analyses have been based on species range maps rather than plant associations.

Although there is considerable debate about the proper scale of analysis and the extent that causal relationships associated with competition and disturbance apply over a range of spatial scales (Huston, 1999; O'Brian, 1998; Whittaker & Field, 2000), there is a consensus that historical factors must be recognized to explain differences in the pool of species present in different

locations that have similar climates (Qian & Ricklefs, 2000), and in the distribution of endemics (Whittaker & Field, 2000). Conventionally, climatic relationships with species diversity are first tested, and if inadequate, historical factors are then investigated. At regional scales, the degree of disturbance and fragmentation of the landscape may still apply, but these factors are generally muted in comparison to climatic effects (see review by Sarr et al., 2005).

Temperature and moisture are the two variables encompassed in most climatic analyses, usually in the form of annual precipitation and evaporation (potential or actual).

Ecologically, one would prefer to analyze climatic effects seasonally and in reference to how organisms directly respond (Mason & Langenheim, 1957). The integrated response of vegetation to climate is expressed as growth, or net primary production, NPP. A direct correlation between productivity and species richness is, not surprisingly, generally better than those derived with annual indices of climate (Hawkins et al., 2003).

The modeling of productivity as a function of climate is embedded in process-based models that predict CO_2 and water vapor exchange as well as the cycling of carbon and nutrients within and through ecosystems (see review by Landsberg, 2003). Through sensitivity analyses, the relative importance of various climatic factors on production can be assessed and mapped spatially (e.g., Nemani et al., 2003). Such process-based models include seasonal water balances and recognize the importance of radiation interception and utilization by vegetation. Process-based growth models are particularly well developed and tested for forests, which leads us to the premise: *That tree diversity should be predictable if dependent on current climatic patterns. The extent that such relationships remain viable under a rapidly changing climate, however, will require periodic retesting.*

We are fortunate in the United States to have access to survey records acquired by the Federal Inventory and Analysis (FIA) program (http://www.fia.fs.fed.us/) that systematically record the composition of forest vegetation across the country. These surveys are much more accurate than species range maps and offer a sound basis for developing and testing correlations between tree richness and productivity at different spatial scales, now and in the future.

Although the productive capacity of the land can be fairly accurately predicted with process-based models if sufficient information on soils and climate is available (Coops & Waring, 2001; Coops et al., 2001; Ollinger et al., 1998), such information is often lacking or is imprecise (Swenson et al., 2005). Alternatively, we might consider modeling GPP, as it is approximately twice the value of NPP (Gifford, 2003; Waring et al., 1998). In the states of Oregon and Washington, GPP, estimated from extrapolation of climate and soil data, accounted by itself for 80% of the observed variation in tree richness at a spatial resolution of 10 km (Swenson & Waring, in press).

Satellite-derived estimates of gross primary production (GPP) are readily available as products generated using NASA's Moderate Resolution Imaging Spectroradiometer (MODIS). Alternatively, we chose to use the MODIS enhanced vegetation index as a surrogate for GPP that is independent of climatic data and therefore accurate, without extrapolation to a spatial resolution of 1 km. Both estimates of GPP are in general agreement where they have been compared with values generated at sites where CO_2 and water vapor exchange were continuous monitored (Rahman et al., 2005).

In this paper we test the extent that EVI correlates with tree richness data from 65 recognized ecoregions across the contiguous U.S.A. where FIA survey data were adequate to predict the pool size of tree species present.

2. Methods

2.1. Ecoregions

To obtain a general description of the ecological zones across the contiguous USA we chose the level III classification of ecological regions of North America available from the US Environmental Protection Agency (http://www.epa.gov/wed/pages/ecoregions.htm). Earlier attempts at classifying ecoregions proved too broad in that many species were included in ecoregions with ranges that did not overlap. The level III classification defines 84 ecoregions within the boundaries of the 48 contiguous states at an approximate scale of 1:30 million. We tested the assumption (CEC, 1997) that each ecoregion could be considered unique, based on similarities in climate, geology, landforms, and flora by confirming that as few as 200 survey plots would provide a good estimate of the total pool of tree species present within an ecoregion.

The amount of forested area varies considerably by ecoregion. To ensure that only forested pixels were used in the analysis, we utilized a second land cover data set derived and distributed as part of the MODIS standard data products. This land cover classification (MOD12Q1, Collection 3, developed by the University of Maryland, UMD (Carroll et al., 2003; Hansen et al., 2000), is also utilized in the analysis of the MODIS GPP product (Zhao et al., 2005). The UMD classification is pixel-based at 1000 m spatial resolution and defines 15 classes covering the major biomes across the globe. To restrict our analysis to forested environments, we combined five forest classes (evergreen needleleaf, evergreen broadleaf, deciduous needleleaf, deciduous broadleaf, and mixed forests) into one mask which was then applied in all subsequent processing. The UMD classification is relatively stable, a desirable feature for our analysis because tree survey data are acquired over a decade.

2.2. Tree richness data

Tree richness values for ecoregions were computed from a total of 174,207 FIA field surveys (44,408 fixed and 129,799 variable area plots). The number of FIA plots present averaged 1540 per ecoregion with a range from 0 to 18,982 across the 84 ecoregions.

To attain a good estimate of tree richness for the largest number of ecoregions, we restricted our analysis to 65 ecoregions with 200 or more FIA field survey plots. With a sample size of 200, an asymptote in species number was

generally approached where there was <1% increase in species number with an addition of 10 plots and a log-linear relation between sample size and species richness accounted for ∼95% of the variation .In two ecoregions, a slightly larger sample was required to meet the standard. Only in ecoregion 19, representing diverse topography in the Waschatch and Uinta Mountains of Utah, were we unable to obtain an r^2 above 0.88 using the full complement of 1505 plots.

2.3. MODIS EVI data

The Moderate Resolution Imaging Spectrometer (MODIS), on board NASA's TERRA (since 2000) and AQUA (since 2002) satellites, is designed to address questions about global carbon dynamics (Heinsch et al., in press). These sensors provide near daily coverage of the globe at a range of spatial resolutions. With 36 spectral bands on each instrument, a number of MODIS products have been developed to characterize atmosphere, ocean, and land surface properties (Justice & Townshend, 2002; Justice et al., 1997). Together, these MODIS products provide significant refinements in spectral, radiometric, and geometric properties compared to previously available data sets with similar spatial resolution (Justice & Townshend, 2002; Zhang et al., 2004).

Two vegetation indices are routinely produced from the MODIS sensor. For our investigation we chose the enhanced vegetation index, EVI, instead of the more widely used normalized difference vegetation index, NDVI. EVI is less sensitive to soil and atmospheric effects than NDVI because it incorporates blue spectral wavelengths. As a result, EVI remains sensitive to increases in canopy density beyond where NDVI becomes saturated (Huete et al., 2002). EVI is calculated as:

$$\text{EVI} = G\frac{\text{NIR} - R}{\text{NIR} + C_1 R - C_2 B + L}$$

where NIR, R, and B are reflectances in the near infrared, red, and blue bands respectively; C_1 and C_2 are aerosol resistance coefficients; G is a gain factor, and L is the canopy background adjustment that addresses nonlinear, differential NIR and red radiant transfer through a canopy. The coefficients adopted in the EVI algorithm are, $L=1$, $C_1=6$, $C_2=7.5$, and $G=2.5$ (Huete et al., 2002).

MOD13 EVI images, composited at 16-day intervals, were downloaded in tiles at 1-km resolution for the period between June 2000 and December 2004 for the contiguous United States, and mosaicked together using the MODIS re-projection tool. A 16-day composite interval has proved adequate to smooth out short-term variations in atmospheric properties and registration errors while offering sufficient resolution to capture trends over the growing season (Rahman et al., 2005).

An average EVI product was then produced that further smoothed interannual seasonal variation captured over the period that MODIS data were available.

The EVI performs well and produces consistent values even when the atmosphere has higher than normal aerosols and

smoke (Miura et al., 1998). The EVI also minimizes residual aerosol effects resulting from the dark target-based atmospheric correction (DTAC) utilized in the MODIS surface reflectance products (Miura et al., 2001). In addition, where a heavy atmosphere exists, cloud contamination routines are applied in the MODIS processing of images, reducing the probability of significant bias in the resulting EVI values. Prior to analysis of the images we visually assessed the derived composite EVI values to ensure data quality. In this way we excluded any large-scale patterns associated with cloud contamination.

2.4. Derivation of growing season EVI surrogates for GPP

Many approaches have been developed to interpret phenological events from temporal variation in vegetation indices. From analyses of time series of vegetation indices it is possible to extract key dates, such as the start and end of the growing season. Given that satellite imagery is used to infer these phenological events, we recognize that each pixel represents an aggregate greenness value, which may include, in the case of forests, an overstory of trees, and an understory of shrubs, herbs, and grasses. Although this makes it difficult to distinguish the composition of vegetation, satellite-derived greenness estimates have the advantage of being fairly stable, in spite of local changes in the composition of vegetation associated with disturbance (Franklin et al., 1997; Goward et al., 1985).

Based on previous studies, we identified four separate formulations of the averaged 16-day EVI layers that seemed useful to compare: (1) the maximum, (2) the seasonal mid-point value, (3) the average value for the growing season, and (4) the annually integrated value (Fig.1).

2.4.1. Maximum annual EVI

In the Pacific Northwest, where evergreen coniferous forests generally dominate the landscape, the maximum EVI is closely correlated with mean annual growth of forests (Waring et al.,
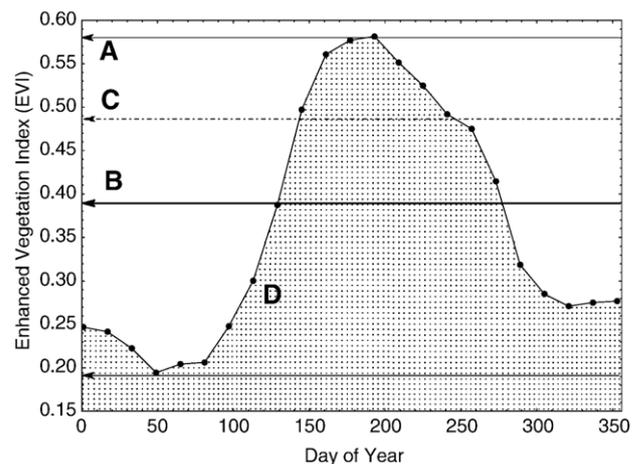

Fig. 1. Graphic representation of the four formulations EVI (derived from 16 day composites) used to predict tree richness: (A) maximum EVI; (B) seasonal mid-point EVI; (C) mean EVI through growing season; and (D) annually integrated EVI. The mid-point values define the beginning and end of the growing season.

2006). This correlation reflects an underlying relationship between the density of canopy that can be supported in any given environment and the photosynthetic capacity of the canopy (Bolstad et al., 2001; McNulty et al., 1996; Waring et al., 1995). Although the maximum EVI is sensitive to recent disturbance, it has the advantage of being unambiguously defined regardless of the type of vegetation present.

2.4.2. Seasonal midpoint EVI

The seasonal midpoint (or half-maximum) EVI was designed to predict the initial leaf expansion of broadleaf forests (Schwartz et al., 2002; White et al., 1997). The method first calculates the annual minimum and maximum EVI for each pixel and the midpoint is then calculated and added to the minimum. This threshold EVI has the advantage over other formulations in that it is sensitive to site-specific variations in the range of EVI and may be more sensitive to local variation in canopy leaf area and chlorophyll concentrations.

2.4.3. Mean growing season EVI

Based on the work of White et al. (2002), we extended the seasonal midpoint EVI technique to define a mean growing season EVI. As indicated in Fig. 1, the seasonal midpoint EVI value represents the threshold above which vegetation is assumed to be actively growing. The date when the temporal EVI sequence crosses this threshold is deemed

the start of the growing season, and likewise, once the EVI falls below the threshold, that defines the end of the growing season. To determine the mean value, we summed the EVI values recorded for each 16-day period above the threshold and computed the mean EVI for the active part of the growing season.

2.4.4. Integrated annual EVI

Goward et al. (1985) demonstrated a linear relation between values of NDVI integrated over a 30 week period and NPP for 12 major vegetation types across North America. We calculated a similar integrated value when EVI was above zero any time throughout the year (Fig. 1).

2.5. Statistical analysis

Statistical models were developed using stepwise linear regression, based on linear and polynomial transformations of total tree richness values and the mean and standard deviation of the four EVI metrics within each of the level III ecoregions (StatSoft, 2000). Models were developed based on summaries from all forested ecoregions with adequate FIA survey data ($N=65$), and those ecoregions containing >50% forested lands. Both linear and non-linear regression models were tested. The most appropriate model was determined based on its standard error, level of statistical significance, and coefficient of determination (r^2).
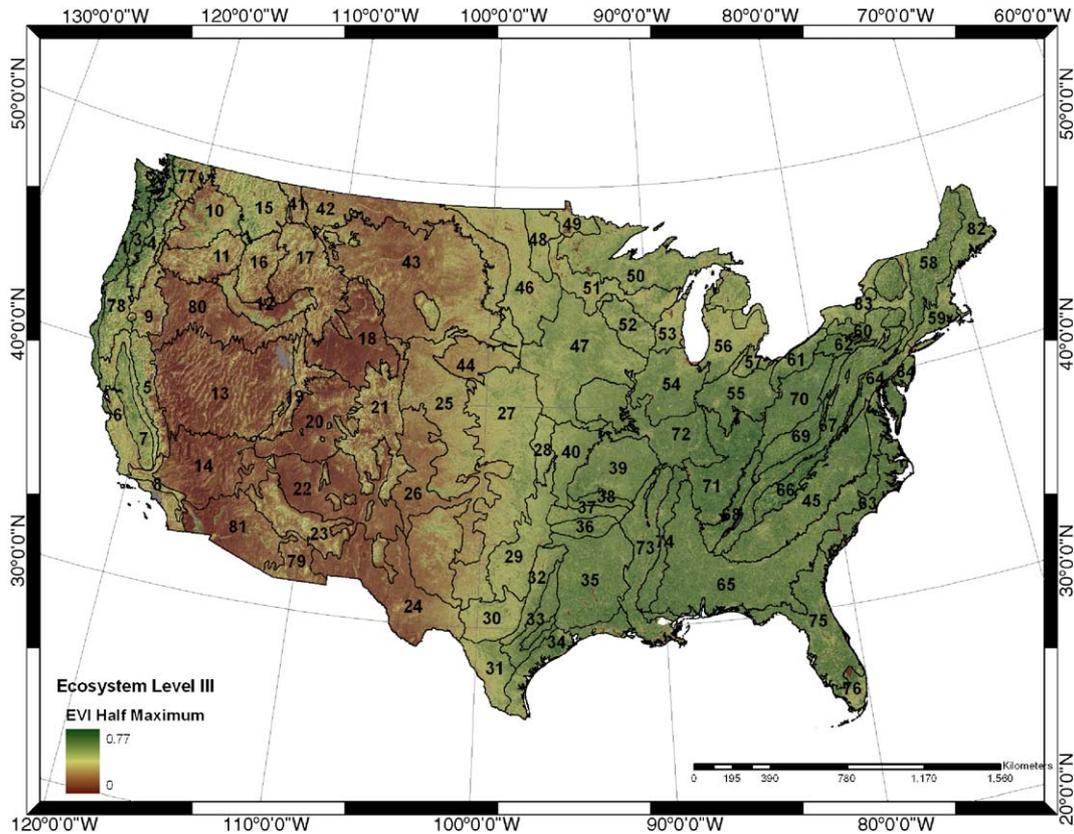

Fig. 2. Mid-point (half-maximum) MODIS EVI derived from 16 day EVI composites (2000–2004). The 84 U.S. Environmental Protection Agency (EPA) level III ecoregions are identified by number with their boundaries delineated.

3. Results and discussion

3.1. Ecoregions maximum EVI values and forest cover

In Fig. 2, where level III ecoregions are mapped and numbered, the seasonal mid-point (half-maximum) EVI values are represented; other configurations of the index present similar patterns. The darker green regions, representing higher values, are concentrated east of the Mississippi River with the exception of the Pacific Northwest and parts of California west of the crest of the Sierra Mountains. More than a third of the 65 ecoregions with adequate numbers of FIA plots had 10% or less of their total area forested (Fig. 3). The likelihood, that reduced forested land area might affect tree diversity within an ecoregion is obviously worth consideration.

3.2. Tree richness patterns and EVI

In the statistical comparison of the four EVI formulations presented in Table 1, we found that the forward-stepwise regression procedure consistently selected a polynomial expression over a linear fit. Although spatial variation in EVI occurs within ecoregions, accounting for this variation did not improve the predictive equations significantly. When data from all 65 ecoregions were included, the four formulations of EVI accounted for between 57% and 63% of the observed variation in tree richness. The four EVI formulations are highly correlated with one another ($r > 0.9$). The model using mid-point EVI values improved the most with exclusion of ecoregions with <50% forest cover, particularly in capturing the high end of tree richness values. The integrated annual EVI did not do quite as well ($r^2 = 0.76$ vs. 0.80), perhaps because in areas where temperatures drop below freezing, evergreen vegetation still exhibits a high EVI value. Excluding ecoregions with <50% forest cover consistently improved the prediction of tree richness with all EVI formulations to the

Table 1
Statistical evaluation of different functions of EVI to predict tree richness patterns

EVI Type	Adjusted r^{2*}	Standard error (number of species)	N
Maximum annual EVI	0.63 (**)	24	65
	0.69 (**)	22	62 (less 1–3)
	0.81 (***)	22	20 (forest >50%, 1–3)
Integrated annual EVI	0.62 (**)	25	65
	0.64 (**)	24	62 (less 1–3)
	0.76 (**)	19	20 (forest >50%, 1–3)
Average EVI during growing season	0.62 (**)	25	65
	0.70 (**)	22	62 (less 1–3)
	0.82 (**)	17	20 (forest >50%, 1–3)
Seasonal mid-point EVI	0.57 (**)	26	65
	0.75 (**)	19	62 (less 1–3)
	0.80 (***)	18	20 (forest >50%, 1–3)

Significance (*) 0.05 level, (**) 0.01 level, (***) 0.001 level.
Linear regressions were also tested but accounted for less variation than the polynomial functions.

extent they accounted for ~80% of the variation in tree richness across ecoregions. The polynomial relation between mid-point EVI and tree richness for 62 forested ecoregions is presented in Fig. 4.

Three ecoregions (1, 2, and 3), all located in the Pacific Northwest, stand out as having less than half the tree species predicted by the mid-point EVI model (Fig. 5). Excluding these three ecoregions, all heavily forested, raised the r^2 for the mid-point EVI relation from 0.57 to 0.75 (Table 1). All formulations of EVI significantly overestimated tree richness in these three ecoregions (e.g., compare Fig. 6A with B), as did analyses based on species range maps and correlations
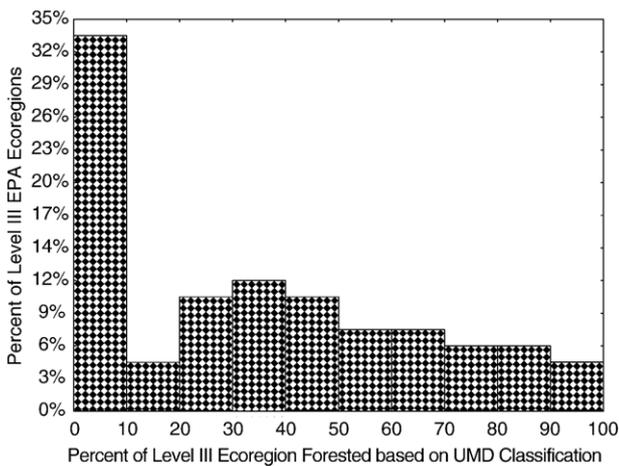

Fig. 3. The area forested within the 65 ecoregions averaged between 30% and 40%, but >36% of the ecoregions contained <10% forest cover according to the MODIS University of Maryland (UMD) land classification (Carroll et al., 2003).
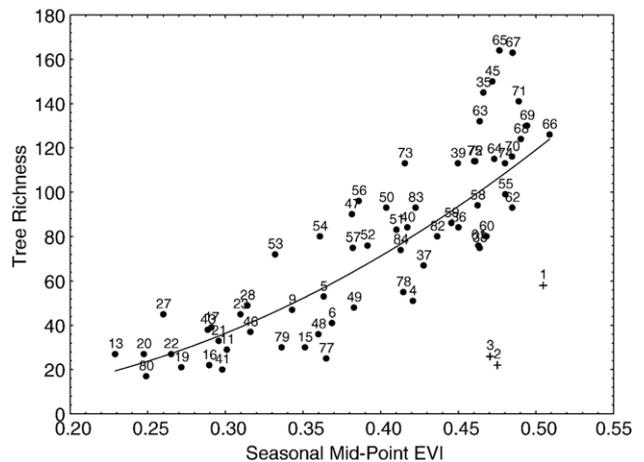

Fig. 4. The seasonal mid-point EVI, equivalent to the value used to define the beginning and end of the growing season, provides the best fit to the data when three Pacific Northwest ecoregions (+), were excluded. $\sum$ Tree $\# = -18.1 + 586 x^2$, where $x =$ seasonal mid-point EVI, $r^2 = 0.75$. The slope of the polynomial regression increases still more when the analysis is further restricted to those ecoregions with >50% forest cover ($r^2 = 0.80$).
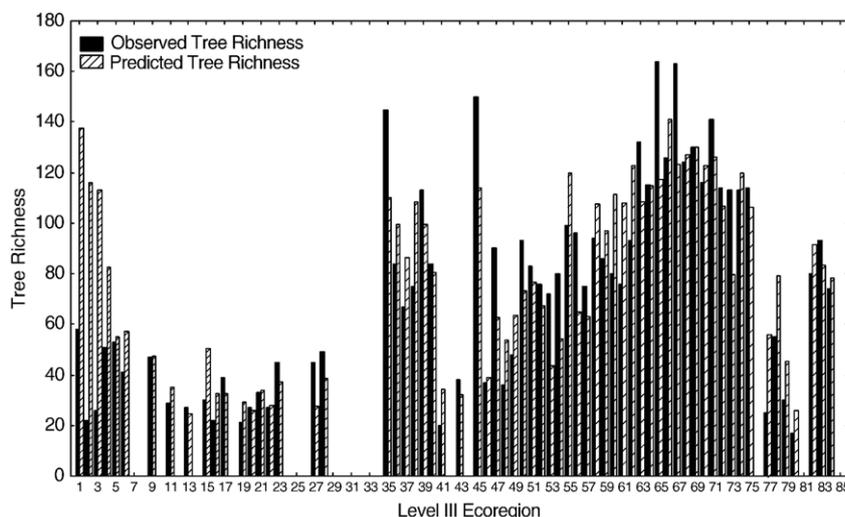
Fig. 5. Although predictions of tree richness vary from that observed in many ecoregions, the over prediction of tree richness in ecoregions 1–3 stands out. These ecoregions are located in the Pacific Northwest where major extinction of the flora occurred under a cooler and drier Pliocene environment than exists today (Waring and Franklin, 1979).

with average annual estimates of water vapor exchange (Currie & Paquin, 1987). In the Pacific Northwest, present climatic conditions are favorable to support a richer flora than is now present. During the late Pliocene, more than 40 Angiosperm tree genera were represented in the flora of the Pacific Northwest, but massive extinction eliminated most of these under a colder and drier environment than exists today (Waring & Franklin, 1979). As Whittaker and Field (2000) suggested, one can identify regions where evolutionary history is of particular importance by the degree that those regions differ from general relations obtained between climatically-related indices and biodiversity.

Ecoregions with >130 tree species (maximum in ecoregion 65 with 164 species, Fig. 5) are located in the southeastern U. S., with regional richness decreasing in all directions (Fig. 6A). West of the Mississippi River, tree species richness is generally low, with less than 30 species in the Southwest (minimum in ecoregion 80 with 17 species, Fig. 5) ecoregions, and fewer than 60 species in California and the Pacific Northwest. The relative errors in predicted tree richness for 65 ecoregions are presented in Fig. 7. The Pacific Northwest represents a region with a much less rich tree flora than predicted whereas the Midwest has significantly more tree species than the model predicts. These differences appear independent of the degree to which forest cover is present because the Pacific Northwest has >50% forest cover whereas the Midwest ecoregions are generally <10% forested. Nonetheless, when the relationship between EVI and tree richness is restricted to areas with >50% forest cover, excluding the Pacific Northwest, all configurations of EVI improve to account for ~80% of the variation, with closer agreement to measured richness values (Table 1).

Initially, we were concerned that variation in the type of forest cover might affect the averaged EVI values derived for each ecoregion. This may be the case for some configurations of the index, particularly the maximum value. In no ecoregion,

however, was one type exclusively represented; on average, the most abundant type represented 68% of the total forest cover. The mid-point EVI, and to a lesser extent the averaged values, take into account differences that may exists in defining the growing season and canopy photosynthetic activity. The annually integrated EVI does not specifically recognize the growing season but is certainly influenced by the presence of deciduous hardwoods.

The general relation between productivity estimated using the seasonal mid-point EVI and tree richness expressed at the ecoregion level was significantly non-linear but not parabolic as has been observed with finer grain analyses (e.g., Swenson & Waring, in press). In finer scale analyses, the most productive and least productive sites are included in the analysis. The possibility that a parabolic relationship between productivity and tree richness was masked by our averaging of estimates of productivity for entire ecoregions will be evaluated in a separate paper based on more detailed analyses at a scale of 30×30 km units. We will also determine the consistency between the EVI-derived estimates of GPP and MODIS products that depend on climate data. If a consistent relationship exists between the two indices of GPP, we would expect concurrent changes in the values with shifts in regional climate. The extent that relationships defined under present climatic conditions remain valid will requires periodic analysis with updated field survey data.

4. Conclusions

Our analysis indicates that a polynomial relation exists between four formulations of EVI and tree richness measured across forested ecoregions in the contiguous U.S.A. We interpret EVI as a good surrogate for productivity. The predictive power of the EVI models increased significantly from ~60% to ~80% when those ecoregions with <50% forested were excluded. Three ecoregions in the Pacific Northwest stood out as exceptions for which all formulations
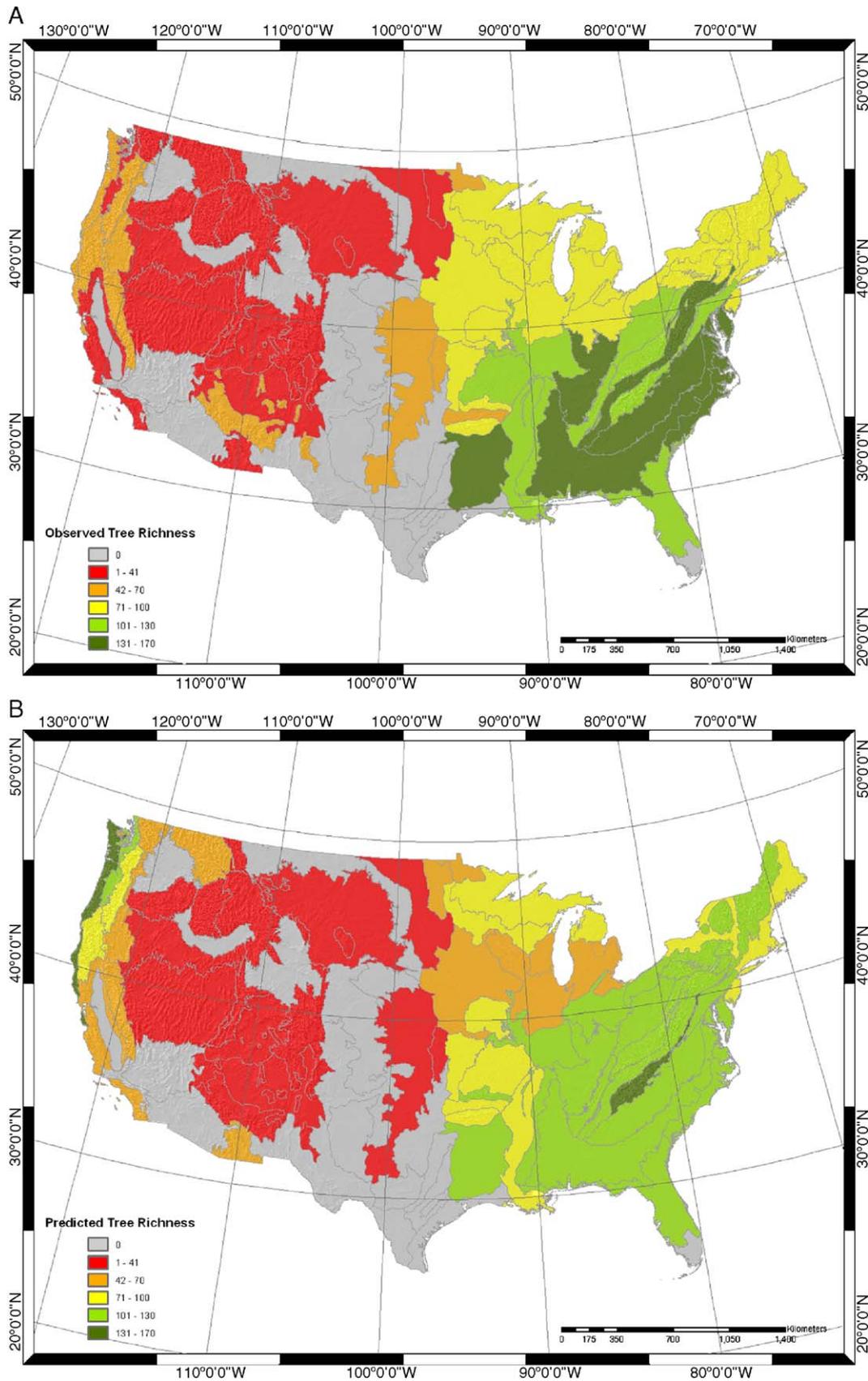
Fig. 6. (A) Map of observed tree richness delineated by ecoregion into 5 classes derived from analysis of ≥ 200 FIA field survey plots in each of 65 ecoregions with forest cover. (B) Map of predicted tree richness delineated by ecoregions into the same 5 classes using the polynomial relation with mid-season EVI shown in Fig. 3. Note that the model consistently overestimates observed tree richness values in the Pacific Northwest region.
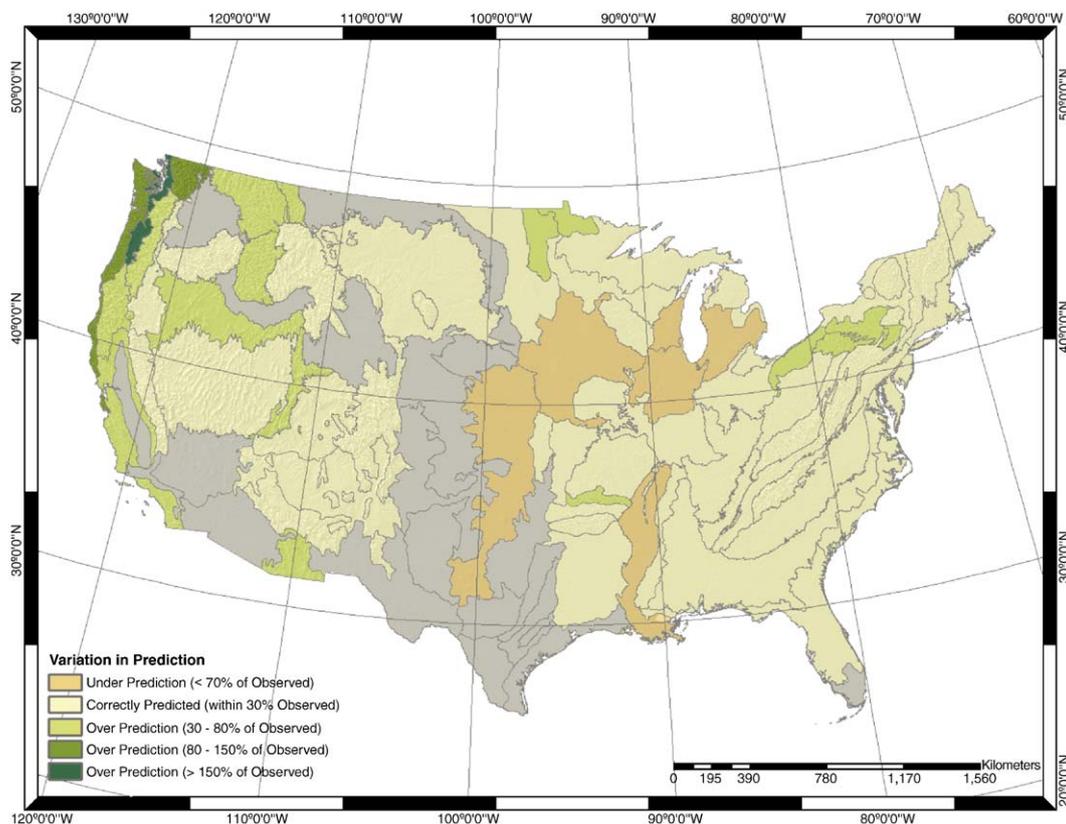
Fig. 7. Deviation in predicted tree richness using the seasonal mid-point EVI formulation for 65 ecoregions with >200 FIA survey plots.

of EVI predicted significantly more species than are present. The evolutionary history of that region offers an explanation for the anomaly. Remotely sensed vegetation indices, such as EVI and the MODIS-derived GPP, offer region-wide estimates of potential productivity that are equivalent, and possibly better than can be obtained from localized field sampling or from process-based models that are dependent on extrapolation of climatic and physiographic information. If relationship between tree diversity and productivity remain viable over time, the establishment of correlations between productivity and tree richness offers promise to help evaluate the effects of future changes in climate at the spatial scale of ecoregions.

Acknowledgments

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